

Growth studies on Norway lobster, *Nephrops norvegicus* (L.), in different areas of the Mediterranean Sea and the adjacent Atlantic*

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SUMMARY: A comparative study of the growth of *Nephrops norvegicus* among different areas in the Mediterranean Sea and the adjacent Atlantic was conducted. MIX and Bhattacharya's length-based methods were used for age determination. Both methods were used for all the studied areas. For the estimation of the growth parameters two non-linear methods, based on the results of the length frequency analysis, were used; the Gauss-Newton method, implemented by the SAS program, was applied using the results of the MIX and the FISHPARM program using the results of the Bhattacharya's method. The identification of the age groups and their mean lengths-at-age as well as the estimation of the growth parameters proved to be difficult. A question regarding the adequacy of the von Bertalanffy model was also posed. Remarkable differences were obvious between sexes in the number of identified age groups and their mean lengths-at-age as well as in their growth parameters in all areas. The comparison of the results obtained for the studied areas showed differences, which could not be considered very important except in the case of the *Nephrops* population of the Alboran Sea, which was characterised by a high growth rate. All other areas seemed to be close; among them the populations from Euboikos Gulf and Catalan Sea being the most different.

Key words: *Nephrops norvegicus*, crustacean, growth, age, length frequency analysis, Mediterranean, Atlantic.

RESUMEN: ESTUDIO DEL CRECIMIENTO DE *NEPHROPS NORVEGICUS* (L.) EN DIFERENTES ÁREAS DEL MEDITERRÁNEO Y DEL ATLÁNTICO ADYACENTE. – Se realiza el estudio comparativo del crecimiento de *Nephrops norvegicus* en diferentes áreas del Mediterráneo y del Atlántico adyacente. Para la determinación de la edad los datos se han analizado utilizando el programa MIX y el método de Bhattacharya. Además, se han utilizado dos métodos no-lineales para la estimación de los parámetros de crecimiento basados en los resultados del análisis de frecuencias de tallas: el método de Gauss-Newton, aplicado a través del programa SAS y FISHPARM. Para el primer método se utilizaron los resultados de MIX y para el segundo los resultados del método de Battacharya. Se notó que la identificación de los grupos de edad y de las tallas medias por edad, así como la estimación de los parámetros de crecimiento, es difícil. Además, se discute la conveniencia del modelo von Bertalanffy aplicado a *N. norvegicus*. Se han encontrado diferencias en todas las áreas de estudio entre los dos sexos, tanto en el número de grupos de edad identificados y sus tallas medias, como en los valores de los parámetros de crecimiento. Sin embargo, la comparación de los resultados obtenidos para cada área de estudio ha mostrado diferencias que no se pueden considerar importantes, excepto en el caso de la población del Mar de Alborán, la cual indica un ritmo de crecimiento más rápido. Todas las demás áreas tienen crecimientos similares, diferenciándose algo más las del Golfo de Euboikos y las del Mar Catalán.

Palabras clave: *Nephrops norvegicus*, crustáceos, crecimiento, edad, análisis de frecuencia de tallas, Mediterráneo, Atlántico.

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INTRODUCTION

The age structure of a population and the growth parameters that characterise each stock constitute basic information for stock assessment. The estimation of these parameters in crustaceans is difficult due to the absence of permanent hard parts, where age can be registered. In such cases, length frequency analysis has often been chosen to estimate mean lengths-at-age and growth parameters (e.g. Farmer, 1973; Conan, 1978; Hillis, 1979; Sardà, 1985). Many approaches exist for the separation of groups in a length distribution. MIX (MacDonald and Green, 1988) and Bhattacharya's (1967) method, applied in this present study, are two widely used techniques that have proved useful in estimating mean lengths of the groups present in length distributions of *Nephrops* (Charuau, 1975; Nicholson, 1979; Figueiredo, 1984; Tully *et al.*, 1989; Mytilineou *et al.*, 1993; Castro, 1995; Mytilineou and Sardà, 1995).

The objective of the present work was a comparative study of growth of *N. norvegicus* among different areas of the Mediterranean and adjacent Atlantic, using the same length-based methods for all the data. It was assumed that any bias that could possibly be introduced by the length frequency analysis techniques used, and arbitrary decisions that such approaches require, will affect all the samples equally, and therefore, the comparative aspects of the study will be valid. Sampling strategies were kept as similar as possible among the different areas.

MATERIALS AND METHODS

Sampling strategy

The data consisted of monthly length frequencies for a period of two years, from October 1993 to September 1995 or November 1995 in some areas. The areas sampled were the south coast of Portugal off the Port of Faro in the Atlantic (P), the Alboran Sea off Malaga (M), the Catalan Sea off Barcelona (C), the Ligurian Sea off Genoa (L), the Tyrrhenian Sea off P.S. Stefano (T), the Adriatic Sea off Ancona (A) and the Euboikos Gulf off Athens (G). In some areas such as Portugal, Malaga, Barcelona and the Adriatic the sampling was kept within a small area in the same fishing grounds and data were obtained in a single fishing trip or within a few days in each month. In the other areas, the monthly samples integrated data from wider areas.

All samples were obtained by commercial bottom trawlers (except in the Adriatic where a research boat was used) and the mesh of the codend was 40 mm except for Greece (32 mm) and Portugal (55 mm). In all cases the length of the carapace (*CL*) was measured to the mm below with digital callipers and the data for males, females and ovigerous females were registered separately. Biological samples were also obtained and one of the aspects studied included the number of soft individuals or individuals with gastroliths as well as the number of mature female, information that would allow an estimation of the moulting and reproduction season for each area. This information was used in some aspects of the length frequency analysis discussed further.

Length frequency analysis

Two independent approaches, the MIX (MacDonald and Green, 1988) and Bhattacharya's (1967) method, were used by two independent teams. In each case the objective was to estimate mean lengths for the age groups present in the length distributions by sex, month and area. Data were used in a different way by each team. Team 1, using Bhattacharya's method implemented in the package FiSAT, entered the data directly as collected, in 1 mm length classes. Team 2, using the program MIX transformed the length frequencies using moving averages of 3 classes on the basic 1 mm length class distributions. This was done to reduce some of the noise introduced by sampling procedures.

Bhattacharya's (1967) method implemented by the Program FiSAT (Gayaniilo *et al.*, 1996) is a method for separating normal components of a distribution with estimation of the mean, standard deviation, separation index (SI; Gayaniilo *et al.*, 1988) and proportions of each one of the components. A valid application of the method presumes some conventions (e.g. $SI \geq 2$, low standard deviations, low X^2 values, regressions created as described by Pauly and Caddy, 1985, etc.). In some cases, these were not accomplished at the same time (especially for X^2). However, this was not considered important enough to reject the analysis, if the identified mean lengths-at-age corresponded to the modes of the distributions (and since X^2 is meaningless with degrees of freedom < 10 , which happened in many cases).

MIX (MacDonald and Green, 1988) is a program that uses a combination of maximum likelihood and non-linear estimation methods for estimation of the mean, standard deviation and proportion of each one of the components of a distribution. In this case, it was assumed that each component was normal. A criterion was established to select the mean lengths-at-age. They were considered to be the ones visually corresponding to the modes in the distributions, and with standard deviations of magnitude not greater than 3 mm. This excluded mean lengths with large standard deviations, attributed to mixtures of more than one age group and which were not possible to separate with length frequency analysis.

Once the well represented groups of each method were detected, a relative age in months was attributed to each mean, guided by the following principles: (a) Components identified in the same sample were considered to be at least one year apart. This assumption derives from the fact that this species has a single recruitment period per year. (b) The mean length-at-age of around 15 to 18 mm, showing up for the first time in the winter-spring, was considered to be age 1. For all the areas, the birthday was considered to be 1st February of the year before. The month was indicated by the biological data. (c) Growth was considered to be of the type modelled by the von Bertalanffy growth curve. Therefore the increment between two consecutive mean lengths-at-age in the same sample should decrease from smaller to larger sizes. This assumption allowed some of the modes identified in the same sample to be discarded or considered more than one year apart. (d) The time of increase in length should coincide with the time of moulting. Hence, information on moulting provided from the biological data was taken into consideration for interpreting the progression of mean lengths over time. For mature females, information from the biological data was also taken into account, assuming that ovigerous females cannot moult. (e) The mean lengths-at-age for the same year class should increase with time in order to follow as clearly as possible the process of growth by means of a modal progression. That means that a mode representing a year class should shift, after one or more moulting (depending on the sex and the maturity state) to a length representing the next mode to the right (assumed to be one year more). For each area, sex and month, a matrix of values of age and length was obtained per method.

Estimation of growth parameters

Growth parameters of the von Bertalanffy (1957) curve were estimated by using non-linear fitting procedures. In one case, when MIX was applied to estimate mean lengths-at-age, the Gauss-Newton method implemented by the program Statistical Analysis System (SAS Institute Inc., 1989) was used. In the other case, when Bhattacharya's method was applied for estimation of mean lengths-at-age, the FISHPARM program implemented by the software package FSAS (Saila *et al.*, 1988) was used. Both approaches to non-linear estimation operate under similar assumptions. In the present study, the analysis was based on the month's data, and not on those of year classes, since modal progression analysis was not considered very useful for growth estimation (Castro *et al.*, 1998).

The growth parameters were estimated by the two methods for each area, sex and month separately. 1) In many cases, the growth parameters estimated by the Gauss-Newton method and SAS program were totally unreasonable. Sometimes extremely high values of L_{∞} and low values of k were obtained. A criterion for acceptance of values was therefore established; only months that fitted the model were accepted. Parameter estimates that produced values of L_{∞} larger than 80 mm for females or 100 mm for males were also dropped. 2) For many months, the results obtained by the FISHPARM program were found unreasonable (L_{∞} lower than the maximum observed length or higher than any value mentioned in published literature - higher than 100 mm for males and 80 mm for females). All the months with unreasonable growth parameter estimates were discarded. Some more criteria were also established; the presence of the younger and older mean lengths-at-age and, the increments between the mean lengths-at-age to be decreasing with age. Once the months with samples containing information for parameter estimation were selected, a global estimate for each area and sex was obtained per method. Moreover, since the estimation of the growth parameters is related to the quality of the analysed sample and the quality of the identified mean lengths-at-age, one more attempt to estimate growth parameters was done using the Bhattacharya's method results, but with more conventions apart from the above mentioned; only samples with a high number of specimens without many gaps in their length composition and absence of gaps between the identified mean lengths-at-age

were used. In this case, only one month producing acceptable estimates and accomplishing, if possible, almost all the above criteria, was used. Finally, the estimation of growth parameters was also attempted using all the identified mean lengths-at-age per studied area for comparison purposes.

Comparison of the data and results

In order to examine the closeness of the studied areas with respect to the mean lengths of the monthly samples, a cluster analysis was applied. Because of the different selectivity of the gears used, only lengths more than 30 mm *CL* were included (the length of 30 mm is greater than *L*₅₀ of the selection curves of the gears used; Sardà *et al.*, 1993; Mytilineou *et al.*, 1998).

Cluster analysis was also used to examine distances between the studied areas with respect to the estimated mean lengths-at-age in the various months. Age 4, one of the best represented in the samples, was selected for the analysis, because it had the highest number of months with data available for all seven areas. This analysis was applied to the results of Bhattacharya's method. In addition, pairwise comparisons of the mean lengths-at-age between areas were carried out by determining the absolute difference between the mean lengths-at-age of two areas, expressed as a percentage of their mean (APD: $(|X_1 - X_2|) 100 / (X_1 + X_2)/2$, where X_1 : mean length-at-age of the area 1 and X_2 : mean length-at-age of the area 2). The mean absolute percentage difference (MAPD: mean of all individual APD values for each area) was also used to compare each area as a whole.

Pairwise comparisons of the growth parameters obtained by the Gauss-Newton method for each area and sex were made using Hotelling's *T*² test for globally comparing the sets of estimated parameters without assuming equal variance-covariance matrices (Bernard, 1981; Hanumara and Hoenig, 1987). The matrix algebra language IML (SAS Institute Inc., 1989) was used to perform the calculations, using as base data the results of the non-linear procedure PROC NLIN (SAS Institute Inc., 1989) as described by Hanumara and Hoenig (1987).

The growth performance index ϕ (Pauly and Murno, 1984) was also estimated for comparison purposes from the growth parameters derived by the FISHPARM program (analysis of selected months). The calculation was made according to the equation: $\phi = \log_{10} k + 2 \log_{10} L_{\infty}$.

Other methodologies

Along with this work, many variations of the described methodologies were tried and abandoned. These included different grouping of the base data, estimation of growth parameters based on the increments of each cohort followed over time, estimation of growth parameters forcing *L*_∞ over given values and the use of the Ford-Walford method (Walford, 1946). When a methodology led to unreasonable results, it was abandoned. The original length data were also used for the direct estimation of growth parameters, applying ELEFAN I (Pauly and David, 1981; Gayanilo *et al.*, 1988) and Shepherd's (1987) method implemented by the FISAT package (Gayanilo *et al.*, 1996). In most cases, *k* was found to be very high, as was *L*_∞ too. The option of choosing or forcing *L*_∞ to more reasonable values resulted in bad fitting curves. For this reason, these two methods were also abandoned.

RESULTS

The monthly length frequency distributions of *Nephrops norvegicus* for the two years of sampling were examined for the various studied areas separately for each sex (distributions not shown here). Table 1 presents information related to the minimum and maximum *CL* of *Nephrops* specimens caught in the different areas during the present study. The examination of the distance between the monthly mean lengths in the various areas showed that for males A, T, L, P and G were close, while C constituted a different cluster and M was even more isolated. For females, A, T, L, P and C were very close, while G a little further apart. M again constituted a very different cluster. The results of this cluster analysis are shown in Figure 1.

TABLE 1. - Minimum and maximum carapace length (mm) of *Nephrops* specimens caught during the two years of sampling in each area for each sex separately.

| AREA | Males | | Females | |
|----------------|-------|------|---------|------|
| | Min. | Max. | Min. | Max. |
| Atlantic | 11 | 63 | 10 | 50 |
| Alboran Sea | 14 | 60 | 13 | 48 |
| Catalan Sea | 11 | 79 | 10 | 66 |
| Ligurian Sea | 12 | 63 | 10 | 55 |
| Tyrrhenian Sea | 16 | 75 | 17 | 60 |
| Adriatic Sea | 20 | 65 | 19 | 54 |
| Euboikos Gulf | 10 | 63 | 11 | 52 |

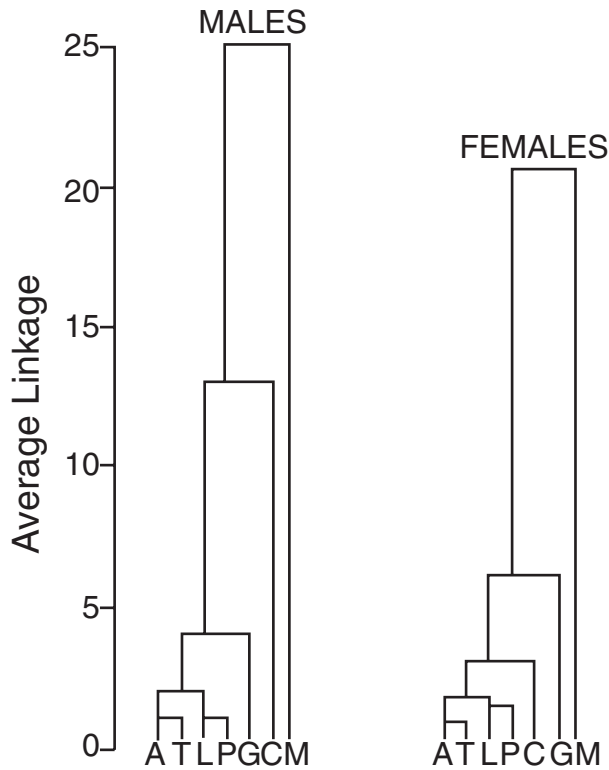


FIG. 1. – Cluster analysis using the Average Linkage method for the examination of the distances between the mean lengths (*CL*) of the monthly samples of the various areas for each sex. Faro in the Atlantic (P), the Alboran Sea off Malaga (M), the Catalan Sea off Barcelona (C), the Ligurian Sea off Genoa (L), the Tyrrhenian Sea off P.S. Stefano (T), the Adriatic Sea off Ancona (A) and the Euboikos Gulf off Athens (G)

In the length frequencies, certain modes appeared more consistently than others. In particular, modes relating to lengths between 25 mm and 40 mm *CL*, appeared in most samples from all areas. These modes presented a continuity over time, indicating that they represented modes related to different year classes and not to moulting activity. However, in some samples the modes were very poorly detected. In Figure 2, two examples, a “good” and a “poor” sample, are shown and in Figure 3 some examples of the continuity of modes over time are presented.

Length frequency analysis was found to be quite difficult and complicated. From all the analyses, it was obvious that the main problem in the length-based analysis was not the selected method, but both the sample structure and the way of applying the analysis (criteria used). All values of the estimated mean lengths-at-age resulting from the two procedures are presented in Tables 2, 3, 4 and 5. The visual comparison of the results of the two procedures (MIX and Bhattacharya’s) showed that, in

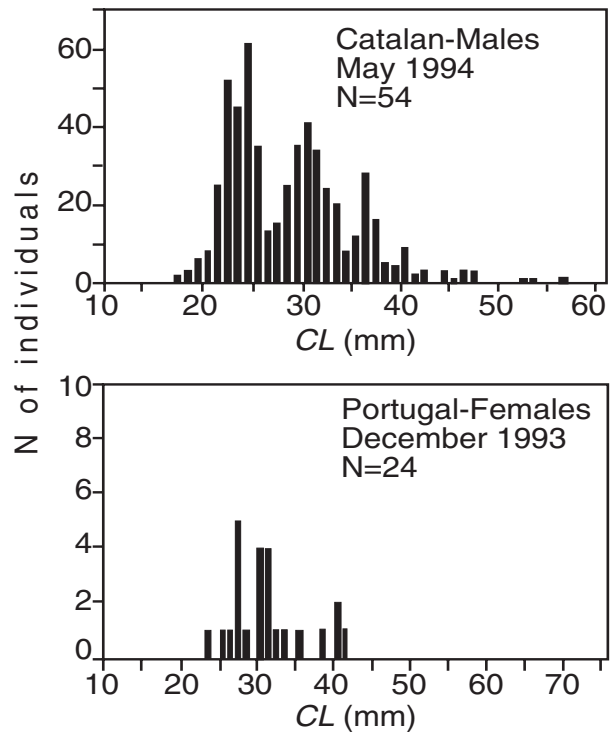


FIG. 2. – Examples of a “good (Catalan-males) and a “poor” (Portugal-females) length frequency distribution. In the first distribution the modes are clearly observed in contrast to the second one. *CL*, carapace length

most of the cases, they were very close. An example of the mean lengths-at-age estimated by the two approaches is presented in Figure 4.

According to Bhattacharya’s method (Tables 2 and 4), the maximum identified number of age groups during the two years of study was for males: 9 for P, 9 for M, 8 for C, 10 for L, 9 for T, 8 for A and 10 for G and for females: 6 for P, 8 for M, 6 for C, 7 for L, 8 for T, 7 for A and 9 for G. In most cases, it was difficult to detect the youngest (0+ and 1) and oldest (>5 for males and >4 for females) age groups. According to MIX (Tables 3 and 5), the maximum identified number of age groups during the two years of study was for males: 7 for P, 8 for M, 8 for C, 8 for L, 9 for T, 8 for A and 11 for G and for females: 6 for P, 8 for M, 7 for C, 7 for L, 6 for T, 7 for A and 8 for G. Again, it was difficult to detect the youngest (0+ and 1) and oldest (>5 for males and >4 for females) age groups in most cases. In both analyses, it was obvious that more age groups occurred in the length frequencies of all areas, but they could not be identified because of their low representation in the samples. In all areas two or three cohorts were well represented and could be followed along most of the samples.

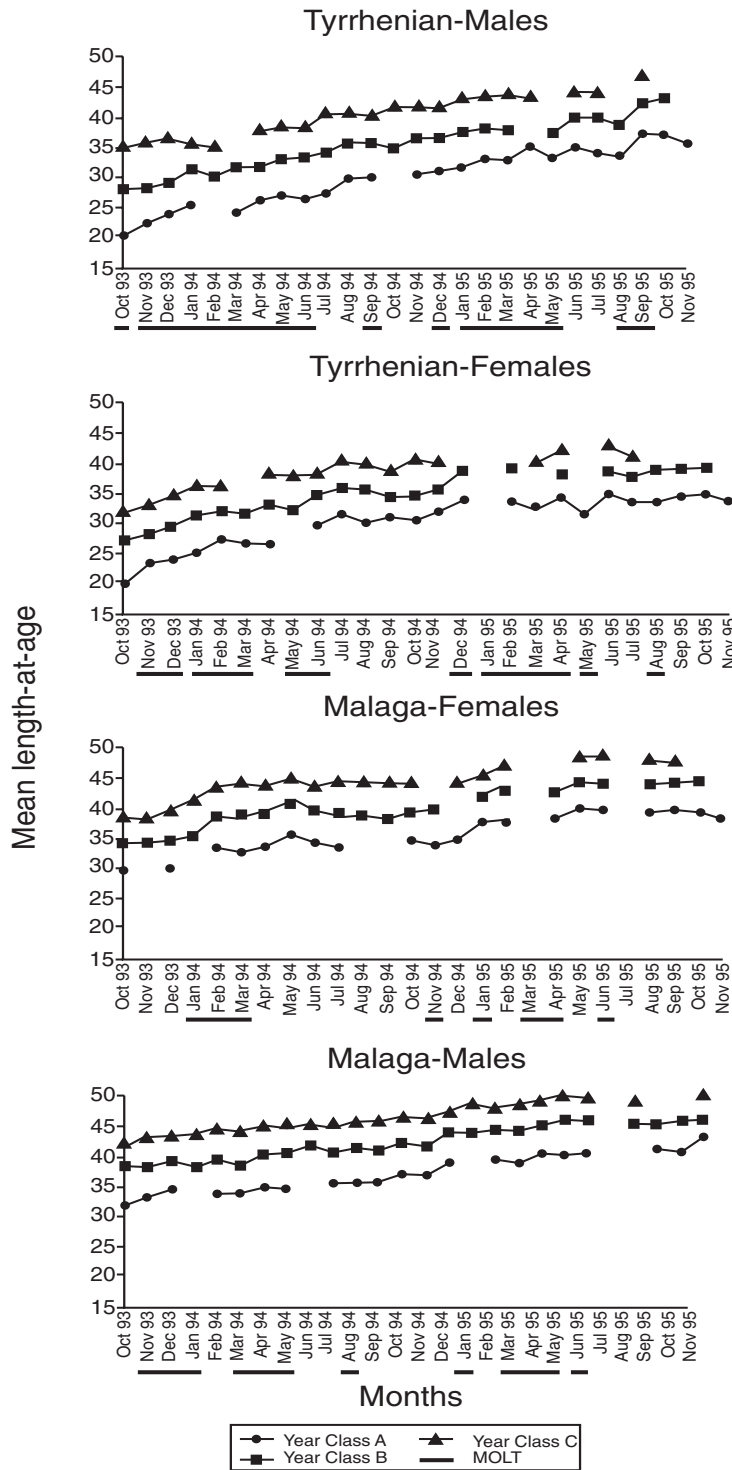


FIG. 3. – Examples of the continuity of modes over time for three year classes (the most representative in the samples). Increase in length is observed after moulting, and is more easily detected in adult females (restricted moulting period) than in males (moulting all the year).

These corresponded well with the two or three modes observed in the length frequencies, reported above. This fact constituted a confirmation for the validity of the mean lengths-at age identified by the length frequency analysis.

The results of the length frequency analyses indicated that differences exist between the sexes in all the areas. The females always presented fewer age groups and lower increments than the males (Table 2, 3, 4 and 5). Regarding the differences

TABLE 2. – Identified mean lengths-at-age of male *N. norvegicus* using BHATTACHARYA'S method and number (N) of examined individuals from Octobe 1993 to November 1995 in the different studied areas.

| | 93 Oct | 93 Nov | 93 Dec | 94 Jan | 94 Feb | 94 Mar | 94 Apr | 94 May | 94 Jun | 94 Jul | 94 Aug | 94 Sep | 94 Oct | 94 Nov | 94 Dec | 95 Jan | 95 Feb | 95 Mar | 95 Apr | 95 May | 95 Jun | 95 Jul | 95 Aug | 95 Sep | 95 Oct | 95 Nov | | | | | | | | | | | |
|---------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| ATLANTIC | 30.91 | 37.31 | 33.34 | 34.41 | 36.00 | 39.79 | 33.89 | 30.44 | 31.90 | 33.34 | 38.93 | 40.10 | 35.29 | 44.83 | 41.76 | 45.90 | 44.83 | 47.70 | 49.80 | 49.59 | 40.21 | 40.88 | 46.22 | 49.93 | 49.32 | 58.00 | 46.30 | 41.84 | 41.84 | 46.30 | 50.34 | 27.52 | 34.45 | | | | |
| N | 586 | 37 | 262 | 73 | 27.91 | 34.50 | 28.00 | 24.50 | 24.00 | 27.61 | 28.00 | 24.33 | 31.59 | 37.00 | 35.39 | 36.00 | 35.51 | 38.11 | 24.00 | 27.51 | 24.00 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | |
| ALBORAN | 34.30 | 32.16 | 41.25 | 28.50 | 27.91 | 34.50 | 28.00 | 24.50 | 24.00 | 27.61 | 28.00 | 24.33 | 31.59 | 37.00 | 35.39 | 36.00 | 35.51 | 38.11 | 24.00 | 27.51 | 24.00 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | |
| N | 586 | 37 | 262 | 73 | 27.91 | 34.50 | 28.00 | 24.50 | 24.00 | 27.61 | 28.00 | 24.33 | 31.59 | 37.00 | 35.39 | 36.00 | 35.51 | 38.11 | 24.00 | 27.51 | 24.00 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | 38.11 | 24.00 | 35.51 | |
| CATALAN | 27.75 | 22.98 | 21.99 | 23.33 | 19.55 | 20.39 | 21.48 | 23.70 | 22.71 | 22.03 | 27.59 | 22.23 | 28.86 | 25.04 | 23.60 | 18.10 | 20.91 | 19.76 | 23.70 | 24.06 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 | 18.00 | 22.88 |
| N | 736 | 198 | 399 | 107 | 414 | 549 | 389 | 333 | 233 | 420 | 202 | 198 | 134 | 110 | 250 | 315 | 388 | 185 | 284 | 125 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | 123 | | |
| LIGURIAN | 16.19 | 23.13 | 29.29 | 35.71 | 41.50 | 41.26 | 46.00 | 44.34 | 45.42 | 44.88 | 49.28 | 53.67 | 54.79 | 58.90 | 58.07 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | 503 | |
| N | 106 | 880 | 681 | 365 | 563 | 194 | 850 | 544 | 919 | 381 | 307 | 503 | 559 | 563 | 472 | 405 | 348 | 361 | 290 | 335 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | 471 | | |
| TYRRHENIAN | 20.70 | 28.18 | 29.09 | 31.31 | 30.19 | 24.25 | 26.27 | 27.00 | 21.73 | 27.33 | 22.50 | 30.00 | 26.90 | 24.75 | 31.00 | 31.70 | 32.82 | 26.04 | 28.29 | 28.17 | 27.90 | 27.62 | 21.51 | 15.67 | 24.84 | 18.50 | 14.00 | 24.79 | 24.83 | 24.79 | 24.83 | 24.79 | 24.83 | 24.79 | 24.83 | 24.79 | |
| N | 251 | 553 | 503 | 97 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | 337 | | |
| ADRIATIC | 22.98 | 25.84 | 26.57 | 16.50 | 15.94 | 17.33 | 19.79 | 20.21 | 15.00 | 17.71 | 23.67 | 15.67 | 15.00 | 16.80 | 16.80 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | 17.42 | |
| N | 1606 | 835 | 630 | 565 | 487 | 202 | 879 | 653 | 788 | 491 | 350 | 853 | 370 | 659 | 402 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | 288 | 275 | | |
| EUBOIKOS GULF | 24.24 | 24.76 | 22.54 | 29.91 | 25.75 | 26.64 | 31.06 | 33.20 | 29.91 | 27.99 | 26.08 | 27.55 | 28.65 | 21.76 | 32.43 | 24.80 | 25.86 | 27.48 | 27.71 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | 27.31 | |
| N | 2254 | 2535 | 1825 | 1200 | 806 | 764 | 375 | 347 | 405 | 344 | 726 | 689 | 1505 | 644 | 402 | 535 | 669 | 297 | 288 | 1102 | 490 | 406 | 286 | 590 | 590 | 590 | 590 | 590 | 590 | 590 | 590 | 590 | 590 | 590 | 590 | | |

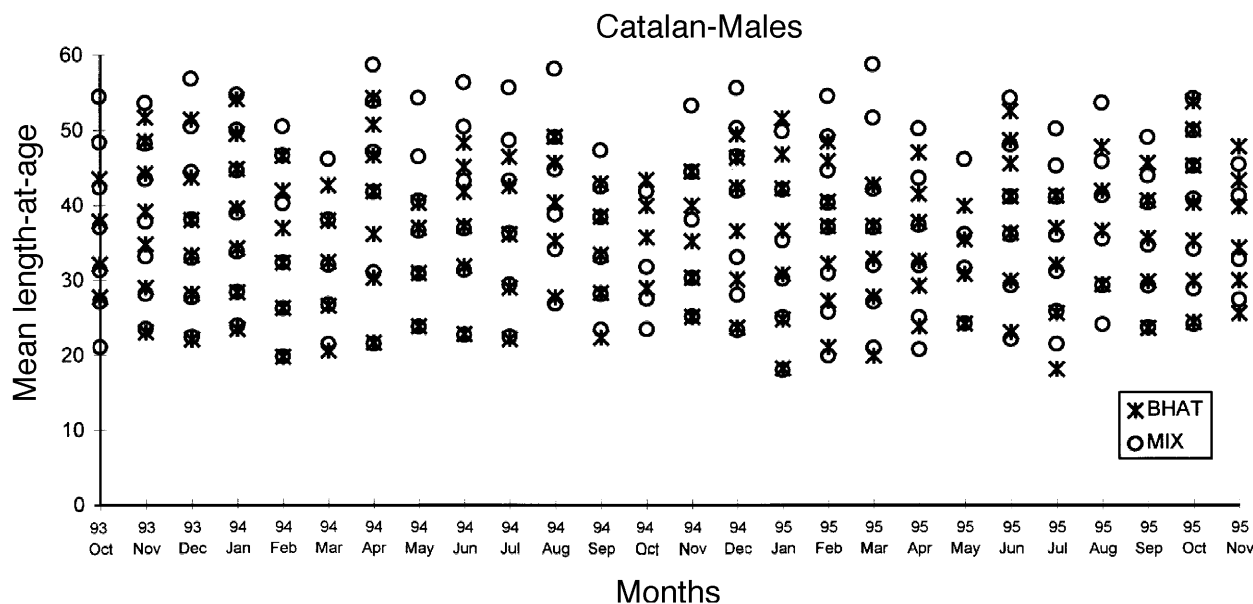


FIG. 4. – Mean lengths-at-age estimated by MIX and Bhattaharya’s method BHAT (only males of Catalan Sea are presented here as an example).

between areas, the examination of the closeness of the mean lengths-at-age in the various months showed that for males L, T, A, G and P were close, whereas C was more distant and M even more so. For females, A, G and L constituted a cluster, and T, P and C another, while M remained the only representative of a separate cluster. Figure 5 presents the results of this analysis. The comparison of the mean lengths-at-age, expressed by the MAPD values, showed similar results. For both sexes, most of the larger MAPD values were between, on the one hand, M and C, and on the other, A, G, P, L and T. The largest MAPD values of all was between M and C. For males, all distances between A, G, P, L and T were low. For females, however, the MAPD distances distinguished two groups, one comprising A, G and L, and the other including T, P and C. T and P were closer to the first group than C. The same was also found for M. The results of the MAPD values are presented in Table 6.

The estimation of the growth parameters in both approaches proved to be difficult. The estimates were not always acceptable. In some cases, the values of L_{∞} were lower than expected (e.g. in Table 7 the case of Malaga) considering the maximum sizes present in the catches (Table 1). On the other hand, the application of the von Bertalanffy growth model presented difficulties. In many samples, the

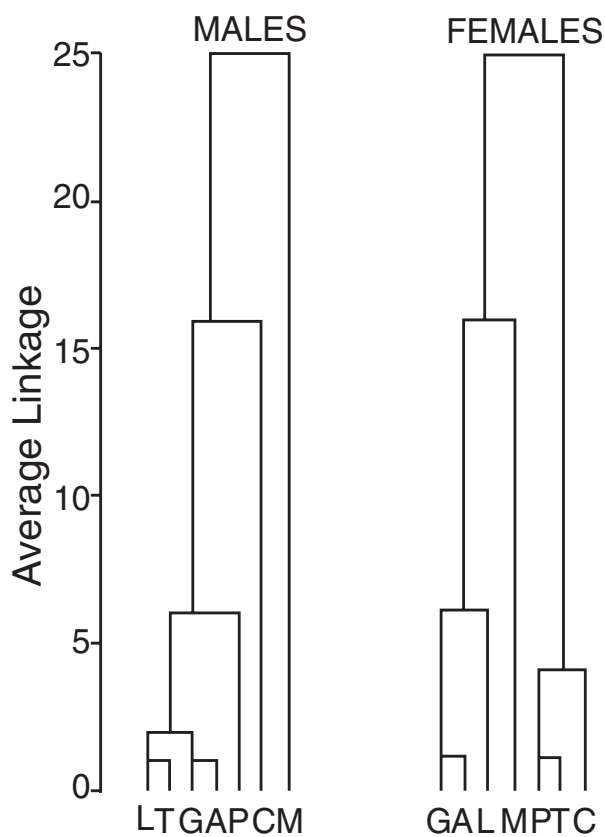


FIG. 5. – Cluster analysis using the Average Linkage method for the examination of the distances between the mean lengths-at-age of the 4 year old age group of the various areas for each sex separately. (P), Atlantic; (M), Alboran Sea; (C), Catalan Sea; (L), Ligurian; (T), Tyrrhenian; (A), Adriatic and (G): Euboikos Gulf.

TABLE 6. – Estimated values for the absolute difference of the mean lengths-at-age expressed as a percentage of their mean (MAPD) between the different studied areas. (P), Atlantic; (M), Alboran Sea; (C), Catalan Sea; (L), Ligurian; (T), Tyrrhenian; (A), Adriatic and (G): Euboikos Gulf. *for the symbol of the area see in the text.

| Males | | | | | | |
|-------|------|------|-----|-----|-----|-----|
| | M* | C | T | P | A | G |
| C | 25.0 | | | | | |
| T | 10.8 | 15.0 | | | | |
| P | 16.6 | 9.1 | 6.2 | | | |
| A | 13.2 | 12.9 | 6.2 | 7.0 | | |
| G | 12.5 | 13.2 | 5.3 | 6.6 | 5.1 | |
| L | 9.6 | 16.5 | 5.5 | 9.3 | 8.0 | 6.8 |

| Females | | | | | | |
|---------|------|------|------|-----|-----|-----|
| | M | C | T | P | A | G |
| C | 21.7 | | | | | |
| T | 16.4 | 6.3 | | | | |
| P | 16.8 | 6.2 | 4.6 | | | |
| A | 7.9 | 13.8 | 9.9 | 8.9 | | |
| G | 8.9 | 13.6 | 10.0 | 9.7 | 6.4 | |
| L | 10.6 | 11.7 | 7.0 | 7.0 | 6.4 | 5.5 |

TABLE 7. – Estimated growth parameters of *N. norvegicus* for each area and sex, using the Gauss-Newton method and SAS program. The table includes also the number of pairs of age-length values (*n*) used to produce the estimates and the Mean Square Error (MSE) value for the fitting.

| Males | | | | | | |
|--------------------|--------------|------|-------|-----|------|--|
| AREA | L_{∞} | k | t_0 | n | MSE | |
| Atlantic (P) | 71.3 | 0.10 | -2.45 | 59 | 1.12 | |
| Alboran Sea (M) | 78.4 | 0.17 | -0.38 | 39 | 0.85 | |
| Catalan Sea (C) | 72.9 | 0.14 | -1.43 | 40 | 1.96 | |
| Tyrrhenian Sea (T) | 80.8 | 0.13 | 0.07 | 61 | 1.63 | |
| Adriatic Sea (A) | 71.4 | 0.11 | -1.18 | 88 | 3.29 | |
| Ligurian Sea (L) | 65.2 | 0.16 | -0.96 | 32 | 2.94 | |
| Euboikos Gulf (G) | 82.4 | 0.12 | -0.01 | 79 | 2.55 | |

| Females | | | | | | |
|--------------------|--------------|------|-------|-----|------|--|
| AREA | L_{∞} | k | t_0 | n | MSE | |
| Atlantic (P) | 62.4 | 0.14 | -1.19 | 39 | 1.79 | |
| Alboran Sea (M) | 59.4 | 0.20 | -0.92 | 49 | 4.99 | |
| Catalan Sea (C) | 54.9 | 0.18 | -1.36 | 38 | 2.06 | |
| Tyrrhenian Sea (T) | 69.4 | 0.12 | -0.64 | 46 | 2.29 | |
| Adriatic Sea (A) | 68.0 | 0.14 | -0.21 | 30 | 1.99 | |
| Ligurian Sea (L) | 54.5 | 0.22 | 0.03 | 37 | 2.78 | |
| Euboikos Gulf (G) | 75.8 | 0.12 | -0.11 | 79 | 2.76 | |

TABLE 8. – Growth parameters of *N. norvegicus* estimated by the FISHPARM program, obtained from the analyses of one or more selected months as well as the analysis of all months for each area and sex. The mean square error (MSE), the growth performance index ϕ' and the number of analyzed months are also presented.

| AREA | Males | | | | | | Females | | | | | |
|--------------------|--------------|------|-------|------|--------|--------|--------------|------|-------|------|--------|--------|
| | L_{∞} | k | t_0 | MSE | ϕ | Months | L_{∞} | k | t_0 | MSE | ϕ | Months |
| Atlantic (P) | 78.9 | 0.14 | -0.56 | 1.30 | 2.94 | 3 | 71.3 | 0.12 | -1.15 | 0.61 | 2.79 | 3 |
| | 83.4 | 0.13 | -0.33 | 0.24 | 2.96 | 1 | 70.7 | 0.12 | -1.36 | 0.29 | 2.78 | 1 |
| | 158.3 | 0.04 | -2.25 | 4.03 | 3.00 | 20 | 90.4 | 0.07 | -2.11 | 2.29 | 2.76 | 20 |
| Alboran Sea (M) | 85.2 | 0.14 | -0.80 | 0.84 | 3.01 | 6 | 75.5 | 0.14 | -0.87 | 1.13 | 2.91 | 6 |
| | 86.8 | 0.14 | -0.84 | 0.13 | 3.02 | 1 | 72.6 | 0.16 | -0.87 | 0.19 | 2.93 | 1 |
| | 91.3 | 0.12 | -1.08 | 1.29 | 3.00 | 25 | 93.9 | 0.09 | -1.61 | 1.94 | 2.90 | 25 |
| Catalan Sea (C) | 85.7 | 0.10 | -0.52 | 2.99 | 2.88 | 7 | 71.4 | 0.12 | -0.53 | 1.05 | 2.79 | 3 |
| | 86.8 | 0.10 | -0.30 | 0.09 | 2.87 | 1 | 67.0 | 0.15 | -0.33 | 0.03 | 2.73 | 1 |
| | 94.2 | 0.09 | -0.81 | 3.06 | 2.89 | 26 | 171.1 | 0.03 | -1.80 | 1.67 | 2.99 | 26 |
| Ligurian Sea (L) | 86.5 | 0.12 | -1.05 | 5.31 | 2.94 | 6 | 67.6 | 0.14 | -0.97 | 1.95 | 2.80 | 3 |
| | 83.2 | 0.12 | -0.87 | 0.04 | 2.92 | 1 | 63.2 | 0.15 | -0.89 | 0.02 | 2.79 | 1 |
| | 89.0 | 0.11 | -1.08 | 4.88 | 2.94 | 17 | 77.4 | 0.11 | -1.32 | 1.48 | 2.81 | 17 |
| Tyrrhenian Sea (T) | 79.9 | 0.13 | -1.02 | 1.30 | 2.91 | 9 | 70.0 | 0.12 | -1.08 | 1.84 | 2.78 | 6 |
| | 81.6 | 0.13 | -0.89 | 0.08 | 2.94 | 1 | 65.0 | 0.15 | -0.76 | 0.28 | 2.80 | 1 |
| | 99.8 | 0.09 | -1.39 | 1.72 | 2.94 | 26 | 87.8 | 0.08 | -1.26 | 2.75 | 2.82 | 26 |
| Adriatic Sea (A) | 83.3 | 0.11 | -1.24 | 1.60 | 2.90 | 6 | 68.5 | 0.14 | -1.02 | 1.37 | 2.83 | 7 |
| | 81.5 | 0.11 | -0.95 | 0.03 | 2.87 | 1 | 67.0 | 0.14 | -0.88 | 0.42 | 2.80 | 1 |
| | 120.8 | 0.06 | -1.92 | 4.56 | 2.95 | 21 | 81.8 | 0.10 | -1.36 | 3.28 | 2.84 | 21 |
| Euboikos Gulf (G) | 86.4 | 0.11 | 0.89 | 2.97 | 2.93 | 6 | 75.7 | 0.13 | -0.89 | 1.94 | 2.87 | 9 |
| | 82.7 | 0.12 | -0.95 | 0.80 | 2.91 | 1 | 73.9 | 0.14 | -0.47 | 0.13 | 2.89 | 1 |
| | 93.2 | 0.10 | -1.10 | 2.79 | 2.93 | 24 | 90.3 | 0.09 | -1.27 | 2.27 | 2.88 | 24 |

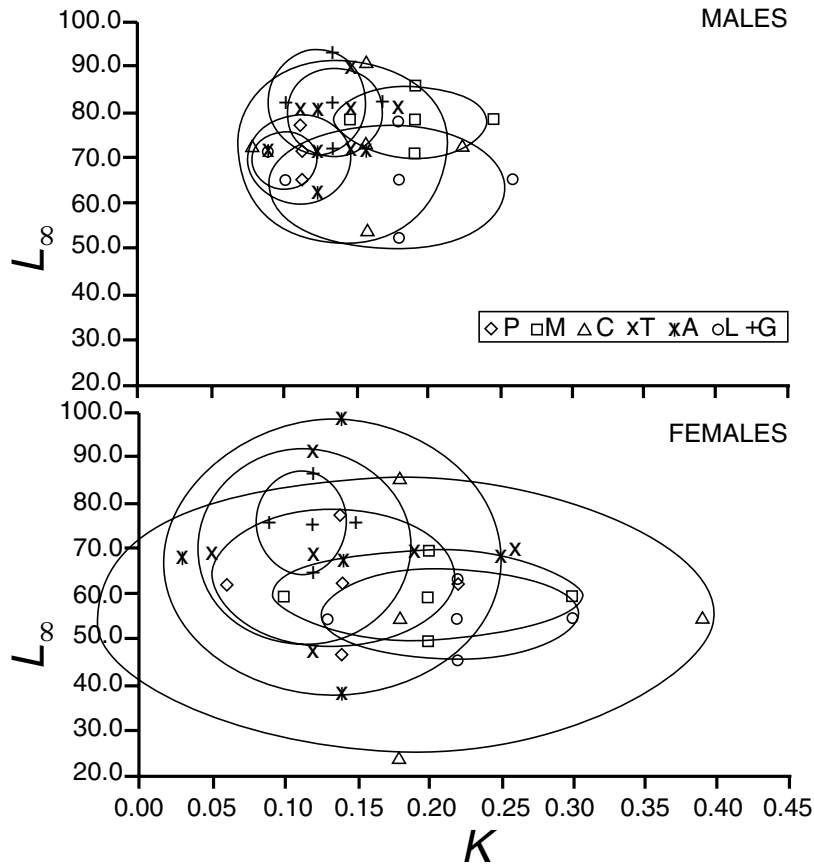


FIG. 6. – Plots of the estimated growth parameters L_{∞} and k and 95% confidence limits are expressed in the form of an ellipse. The height of the ellipse corresponds to the confidence limits for k and the width to the confidence limits for L_{∞} . P: Atlantic, M: Alboran Sea, C: Catalan Sea, L: Ligurian, T: Tyrrhenian, A: Adriatic and G: Euboikos Gulf.

number of age groups identified was small and included only young ages. In other cases the increments between adjacent modes did not decrease from smaller to larger sizes, showing no deceleration in growth, a condition necessary for the application of the model.

The growth parameter estimates for each area and sex using the Gauss-Newton method are presented in Table 7. In Figure 6 are shown the plots of the simultaneous confidence limits of L_{∞} and k . In males, confidence limits were quite narrow, but always overlapped between areas. This was also apparent for females, for which confidence limits were very wide. Table 8 presents the growth parameters values obtained using the FISHPARM program as well as the growth performance index ϕ estimates. The results of three different analyses by the latter method are included in Table 8; those from a selected (as mentioned above) number of months, those from one selected month and finally

those using all months. The growth parameters derived by the first two analyses (analyses based on one or more selected months) were quite close, probably because they were estimated on more or less the same principle. On the other hand, the L_{∞} estimates in the third analysis were always greater (and k values always lower) than those of the first two analyses. This was expected since in the first two analyses only months with decreasing growth increments were selected. The results of the third one, even if they had the advantage of being estimated from more data, were not taken into account, since for the females of all studied areas (except for L) L_{∞} was much greater than 80 mm and for two areas in males (P and A) much greater than 100 mm. Moreover, the second analysis presented the disadvantage of using a lot a conventions and consequently of using very few data. For this reason, it was not taken into account but only presented for comparison purposes, as the previous analysis.

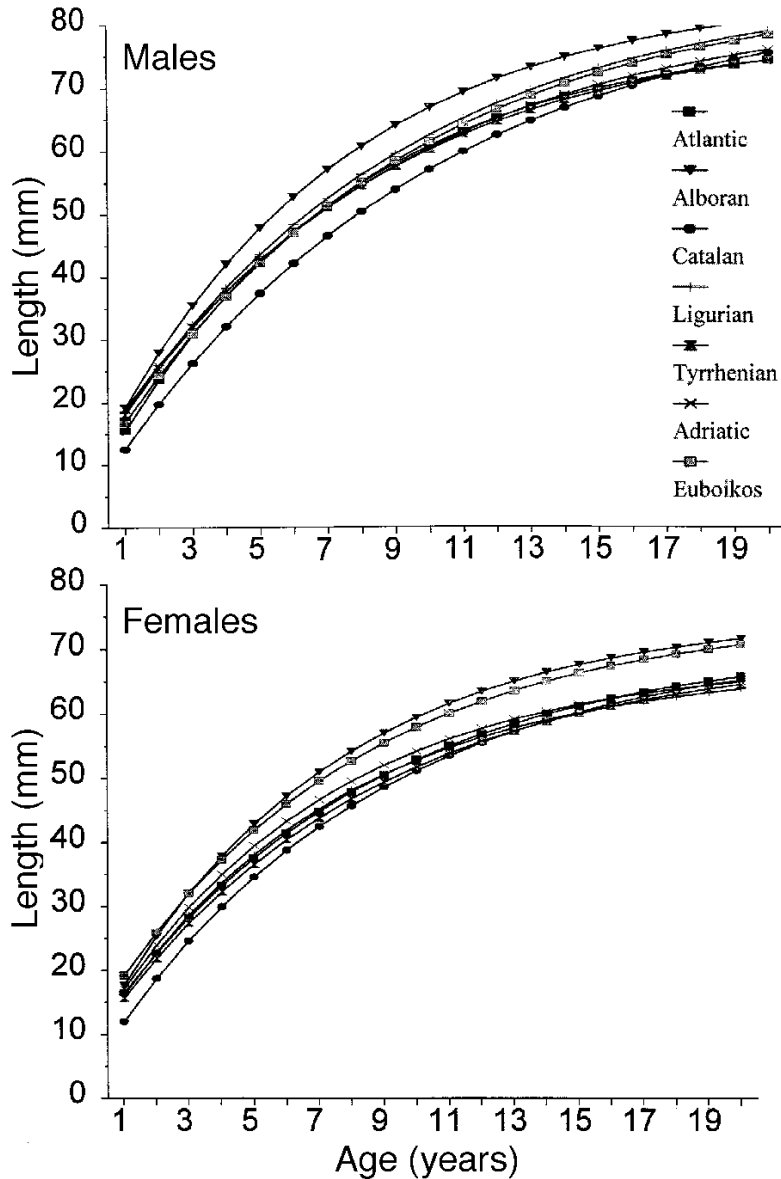


FIG. 7. – Growth curves derived by the FISHPARM program (analysis from selected months) for each area and sex.

The pairwise comparisons of growth parameters, obtained by the Gauss-Newton method, between the different areas (within the same sex) using Hotelling's T^2 test were all significant at the 0.05 level. The visual examination of the growth curves obtained by the FISHPARM program (analysis of selected months), presented in Figure 7, gives an indication of growth differences between the areas. It was observed that for males the curves of M and B were very different from each other and quite different from those of all other areas, which were close. With respect to

females, M showed the most different curve, followed by G. The curves of the other areas seemed to be close. More information regarding the growth curves of the different areas (derived by the FISHPARM program) could be obtained from the ϕ values presented in Table 8. For males, it was observed that the highest value belonged to M (3.01) and the lowest to C (2.88). Other areas showed values ranging from 2.90 to 2.94. For females, the highest value was again in M (2.91), followed by G (2.87). The other areas presented values ranging from 2.78 to 2.83.

DISCUSSION

Length frequency analysis is influenced by many factors. In the present work, a great effort was made to apply this analysis in the most correct way. Since the length-based analysis is applied to length frequencies, their structure is of great importance. Some problems that may affect the structure of length frequencies are as follows. (A) The size of the sample (see for example MacDonald and Pitcher, 1979; Pauly, 1984 cited in Hoening *et al.*, 1987; Erzini, 1990); for this purpose, large samples were collected every month in most cases (>200 individuals per sex each month). (B) Poor sampling of small and large length classes, affecting their representation in the frequencies; this explains the difficulty of identifying the youngest and oldest age groups in this work. From Table 1, the minimum and maximum sizes caught in each area could be compared. (C) Gear selectivity and fishing mortality conditioned by the mesh size are factors influencing the structure of a frequency distribution and consequently the length-based analysis and growth estimation. It must be noted that the mesh size for the sampling in the present work varied between areas. More specifically, in the samples from P (mesh size 55mm), it was difficult to identify the age groups 0+ and 1, while in the samples from G (mesh size 32mm), the youngest age groups were better represented and consequently easier to distinguish. (D) The purity of the samples; it is known that the length structure of *Nephrops* populations change between adjacent areas (Bailey and Chapman, 1983; Anon., 1988; Tuck *et al.*, 1997). For the present work, the samples were collected from a single station in most cases with the exception of T and G, where the sampling covered more than one station, although in a restricted area. (E) The size of class interval (Erzini, 1990); in the present work a 1mm interval was used by both teams, as has already been done by previous authors (e.g. Tully *et al.*, 1989). The same class interval has also been approved by Castro (1990; present work) with simulated data and by Mytilineou and Sardà (1995) with original data as the most adequate for the *N. norvegicus* length frequencies.

Another problem in length frequency analysis is the uncertainty if the different identified components correspond to the real number of age groups composing the populations under study. In the present work, the consideration of the age groups by both teams was done using a series of criteria (see

methods) in order to avoid or limit the subjective interpretation of the results. A confirmation of the accuracy of our results was the continuing presence of some components in the length distributions during the two years of sampling. This fact gave the possibility to follow the different year classes (especially three of them) over time by means of the modal progression. Moreover, the consideration of the different components as age 0+, 1, 2 etc. could be considered reasonable if compared to the information concerning the larval cycle of the species (Farmer, 1973) and the age groups estimated by other authors (e.g. Farmer, 1973; Hillis, 1979; Tully *et al.*, 1989).

Generally, the estimation of the von Bertalanffy growth model parameters requires deceleration of the growth with time. This poses a problem for the adequacy of the von Bertalanffy model, since this was not observed in many cases. If this model is not appropriate for this species, as suggested by studies with simulated data (Castro, 1992; Castro *et al.*, 1998), the removal of data that does not fit the von Bertalanffy model would lead to erroneous results. An alternative could be the use of another growth model, and in fact during some stages of this work the Gompertz model (RZF) was also used. However, the authors suggested that the radical approach of rejecting the von Bertalanffy growth model was not appropriate. First, it is biologically very difficult to consider non-decelerating growth in adult phases. The indications that this may happen in some periods of the life of slow growing decapods are not sufficient yet for retiring the von Bertalanffy growth curve. Such a situation would need evidence from natural populations that is not available. Second, the von Bertalanffy growth curve, even if it is not the best possible model, is easy to apply in fisheries models, it has parameters with biological meaning and easy interpretation, and it is without doubt the most widely used growth model in fisheries. The estimated parameters, even with questionable absolute values when resulting solely from length frequency analysis, be useful for comparative purposes. Since the objective of this project was a comparative study among several areas of the Mediterranean and adjacent Atlantic, the estimation of the von Bertalanffy growth parameters was kept as a means for the data analysis.

In the present work, length frequency analysis presented some difficulties. In certain cases, samples were small and/or their structure did not always permit the detection of the young or old age

groups. Moreover, in any area the whole number of age groups present could not be identified in the length frequency distributions. The progression of modes showed some problems too; the modes presented a variability over time, probably caused by the individual moulting variability. The estimation of the growth parameters was also proved difficult. Their direct estimation, based on the original data using ELEFAN I program and Shepherd's (1987) method, was found unreliable. In addition, modal progression analysis was not considered so adequate for growth estimation (Castro *et al.*, 1998). The indirect estimation of the growth curve from the mean lengths-at-age, using the Gauss-Newton method and the FISHPARM program provided better results, although they were not always acceptable. The estimation of L_{∞} became difficult, and if L_{∞} is underestimated, k will necessarily be overestimated with all the consequences in subsequent use in assessment models. The alternative to this problem would be to force L_{∞} to be a chosen value. In this case, the estimation of k would have little meaning, as discussed by Knight (1968). The problem was probably related to the absence of information for older ages. If only younger ages are present, large standard errors result for the parameters. This is expressed in Figure 6, where males have estimates of growth parameters with much narrower confidence limits than females. This may be the result of better representation of older ages in the catches of males, since no significant behavioural changes during the year, absence of synchronised moulting, slow progression of mean lengths-at-age and faster growth characterise this sex. All these aspects make the estimation of male growth parameters easier and more accurate. Females show very wide ranges for the estimated parameters, a sign of poor results for this sex. Some of the facts that contribute to this may include behavioural aspects and difficulty in separating ages during the moulting season. Behavioural patterns affect the population structure since the catchability to the gear decreases for ovigerous females hidden in their burrows. For age classes that do not reach 100% maturity, this could result in bias in the estimation of mean lengths-at-age during the ovigerous season. After hatching of the larvae, mature females are well represented in the catch, but this is also the period when moulting occurs. During the moulting season it will be very difficult to separate ages because a given individual starts in one mode and ends in the next one, while still belonging to

the same age group. When attributing ages to the identified groups along the moulting period, bias will necessarily occur. We believe that these difficulties are shown in the wide confidence limits both for L_{∞} and k of females (Fig. 6). The differences in the biology of the two sexes is a fact already discussed by various authors (e.g. Farmer, 1973; Charuau, 1975; Hillis, 1979; Sardà, 1985; Anon. 1988). Because of all the above mentioned problems, the approach for the estimation of growth parameters should be the identification of modes within each sample and the combination of data that are not greatly affected by factors such as moulting and behaviour. If growth parameters are used for stock assessment and management purposes, perhaps ranges of values, not point estimates, should be taken into consideration.

With respect to the differences between areas, from all the analyses (distance between the mean CL of the monthly samples, distance between the mean lengths-at-age and MAPD) it was obvious that, the majority of the areas gave very close results for males. Only the Alboran and the Catalan Seas differed from the other areas with the greatest distance between them. The results for females were not so clear. The examination of the similarity of the different areas based on the examination of the mean CL , showed that the Alboran Sea was very different from all other areas (Fig. 1). When the analysis was based on the mean length-at-age, Alboran Sea constituted again a separate group, but two more groups were also detected; one consisting of Adriatic, Ligurian and Euboikos Gulf and the other of Catalan, Tyrrhenian and Atlantic (Fig. 5). This was also found by the examination of MAPD values (Table 6).

The differences in growth parameters between areas were found to be statistically significant in all cases for both sexes. However, it was doubtful if they were also biologically significant. For male *N. norvegicus* (excluding the Ligurian Sea which had quite less information available), all estimates of L_{∞} obtained by the two approaches (Gauss-Newton and FISHPARM) were between 71 and 87 mm (Table 7 and 8), a narrow range taking in consideration the differences in population structure shown in the studied areas and the results of other researchers. Bailey and Chapman (1983) found for two *Nephrops* populations a wider range for males' L (68.9 mm and 46.6 mm). Even for the sub-populations of a small area, Tuck *et al.* (1997) found a greater difference (from 45.3 mm to 65.1 mm) comparing with that of the present study. The plotting of the growth curves

revealed that for males all curves were very close, except in the case of Alboran and Catalan Seas (Fig. 7). This was also observed by the ϕ values (Table 8) with the highest value corresponding to the Alboran and the lowest to the Catalan Sea. In the case of females, for which the results were not so accurate, the curve for the Alboran sea was the most distant, followed by Euboikos Gulf (Fig. 7). They generally were close to each other, however, Alboran Sea showed the greatest value, followed by Euboikos Gulf. For the other areas the ϕ values were found to be very similar. Furthermore, it must be pointed out that the results from the visual comparison of growth curves coincided with those from the examination of the mean *CL* among areas. This is in accordance with the results of Tuck *et al.* (1997), which found that the mean *CL* is positively correlated to L_{∞} and therefore it could be used as an indicator of growth variability.

In summary, the results of this work generally lead us to suggest that, differences exist in the growth pattern of *N. norvegicus* between the different studied areas of the Mediterranean Sea and the adjacent Atlantic, although these could not be considered very important, with the exception of one area. It was clear that *N. norvegicus* from the Alboran Sea presented a great difference in its growth pattern compared with all other areas. For the Adriatic, Tyrrhenian, Ligurian and Atlantic great similarities were found in all analyses. Very close to them was also the Euboikos Gulf (with respect to the males) and the Catalan Sea (with respect to the females). Differences or similarities between areas are probably related to environmental factors (sediment, temperature, etc.) and biological factors (density, availability of food, etc.), the subject of future work by the authors.

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